THE ARRANGEMENT OF SUCKERS ON OCTOPODID ARMS AS A CONTINUOUS CHARACTER

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ABSTRACT

Studies of octopodid taxonomy and classification have cited the number of longitudinal sucker rows on octopus arms as if it were a purely dichotomous character. This character, however, has been suspected to be continuously distributed and associated with increased sucker density (Hoyle, 1886; Berry, 1914). This study tests that hypothesis by comparing the relationship between the mean number of suckers per arm to mean arm length among octopodid genera occurring above 500 m depth. Specimens of genera typified by a single sucker row but with suckers arranged in a zigzag pattern are also included.

Most specimens with two sucker rows and with suckers arranged in zigzags have more suckers at a given arm length than do specimens with suckers arranged in a single row, supporting the hypothesis. Most specimens with one sucker row are separated from those with two rows by a curve on the plot of the number of suckers versus arm length, although four specimens of *Pareledone* spp., preserved with their arms straightened into a swimming position rather than recurved, and the holotype of *Aphrodoctopus schultzei* are exceptional. The number of suckers on the arms of these specimens predict that they will be arranged in one row. The zigzag arrangement seen on the specimens may be due to preservation artifact in the case of the specimens of *Pareledone* and in *A. schultzei* by the 6–8 enlarged suckers on each arm. Variation in the number of suckers within groups defined by the number of sucker rows is greater than that between groups, suggesting that the number of sucker rows is a continuous character. Evidence provided here indicates that *A. schultzei* should be included among the species of *Eledone*.

Key words: Octopodidae, sucker rows, classification, continuous character, *Eledone, Aphrodoctopus*.

INTRODUCTION

Octopodid taxonomy and systematics is entering a dynamic period; preliminary attempts to reconstruct evolutionary relationships among members of the Octopoda (Voss, 1988; Voight, 1990) have lead to a reassessment of our assumptions about the group (Voight, 1991, 1993; in press). One such assumption, expounded by Voss (1988), is that the number of longitudinal sucker rows on the oral surface of the octopus arm is a dichotomous character that accurately reflects evolutionary relationships.

Whether suckers on an octopus arm form one or two longitudinal rows has featured prominently in diagnoses of octopod families (Rochebrune, 1884; Joubin, 1918), subfamilies (Voss, 1988), and genera (e.g. Robson, 1932; Roper & Mangold, 1991). Statements such as in young *Eledone* "as suckers are added they never form two rows" (Hochberg et al., 1992: 265; similarly, Rochebrune, 1884) reflect the degree to which the character is thought to be dichotomous. Yet, the arms of specimens of *Eledone* and *Parele-done* sometimes carry suckers arranged in double rows, or in a zigzag pattern where the number of rows is arguable (Hoyle, 1904; Joubin, 1905, 1918; Gravely, 1908). Preservation may contribute to the formation of double sucker rows in these genera (Guérin, 1908), but live animals also show sucker arrangements considered to be anomalous for their taxon (Chadwick, cited by Gravely, 1908; Naef, 1923).

Whether the number of sucker rows on an octopus arm is a valuable character for reconstructing phylogenies has been questioned (Owen, 1881; Hoyle, 1886; Berry, 1914; Naef, 1923). Based on his discovery of only slight differences in the sucker musculature between specimens of *Octopus*, with two sucker rows, and those of *Eledone*, with one sucker row, Guérin (1908) doubted that sucker arrangement was an adequate basis on which to distinguish the genera. Berry (1914) suggested that octopus suckers are inherently organized in a single row and that only because of crowding are suckers displaced alternately to the side. He felt that this displacement created the appearance of a double sucker row.

The biological significance of this character had yet to be evaluated despite this alternate hypothesis.

This paper tests the hypothesis that sucker crowding is associated with the formation of double sucker rows by examining the relationship between the number of suckers on an arm and arm length among octopodid genera typically occurring above 500 m depth. Specimens of taxa characterized by one sucker row that have suckers in a zigzag arrangement are predicted to show the same pattern as taxa with two sucker rows. The phylogenetic significance of sucker arrangement is assessed.

MATERIALS AND METHODS

To test the hypothesis that the formation of double sucker rows is associated with sucker crowding, the number of suckers on octopus arms with one sucker row was compared to that with two sucker rows as a function of arm length. The hypothesis predicts that more suckers will occupy arms with two rows than with one row at the same arm length. Specimens of taxa typified by one row with suckers arranged in a zigzag pattern will reflect the pattern shown by specimens with two sucker rows.

Specimens included in this analysis (n = 142) were from the California Academy of Sciences, San Francisco; Field Museum of Natural History, Chicago; Rosenstiel School of Marine and Atmospheric Science, University of Miami; the United States National Museum, Washington, D.C.; and University of California Museum of Paleontology, Berkeley. Octopuses with suckers arranged in a double row were represented by specimens of *Octopus*, *Hapalochlaena* and *Macrotritopus* and the type specimen of *Macrochlaena* (Robson, 1926). Data from Toll (1988) for *Cistopus*, *Pteroctopus*, *Robsonella* and *Scaeurgus* and from Roper & Mangold (1991) for *Aphrodoctopus* increased the number of genera with two sucker rows included. Data from Toll (1988) also increased the data available for species of *Octopus*.

Representing octopuses with suckers arranged in a single row were typical specimens of the genera *Eledone*, *Pareledone*, *Vosseledone*, and *Tetracheledone*. To ensure complete and unbiased representation of the taxa, eight data points for *Pareledone* were taken from reports of Joubin (1905), Berry (1917),

Adam (1941), Taki (1961) and Kubodera & Okutani (1986); seven points for *Eledone* were from Massy (1916), Rees (1956) and Adam (1951, 1984). Three specimens of *E. cirrhosa* and data from the type of *P. turqueti* (Joubin, 1905), all with suckers in a zigzag arrangement, were included. Only taxa with mean depth distributions above 500 m were included to avoid the effects of decreased sucker size associated with increased depth distribution (Voight, in press).

Suckers were counted as described by Toll (1988), using a combination of macroscopic and microscopic techniques. Suckers on right arms I-IV were counted; left arms were used if the right were damaged. Only normal arms were used for data analysis; injured arms or those with incomplete regeneration were excluded. Hectocotylized arms of males (one of the third pair of arms specialized for spermatophore transfer) were considered separately from normal arms.

The analysis requires that each datum be independent, that is, free of any correlations or association with other data in the analysis. Because all non-hectocotylized arms of an individual specimen are subject to identical genetic and environmental variables or controls, they are not independent. Statistical tests of the working null hypothesis, that each normal arm of an individual specimen has the same number of suckers, were prohibited by the small sample size within an individual, inevitable errors in counting, and errors in regeneration that may have failed to restore all suckers. This hypothesis was rejected if the number of suckers on different arm pairs varied consistently in all available specimens of a given species.

Only male specimens of *Eledone caparti* were available, and only in this species was the null hypothesis rejected, as indicated by Adam (1950). Typical of *Eledone*, these males have sucker-derived modifications at the arm tips (Haas, 1989: Fig. 2). When the number of modifications and suckers were summed, the result was virtually invariant within an individual (Table 1). Because within individual specimens of all other species examined, the number of suckers was essentially equal among the arm pairs, data taken from only one or two arms were considered representative and were included.

Despite the anomalous pattern seen on arms of *E. caparti*, sucker counts of males with heteromorphic arm tips were represented in the analysis by mean sucker num-

TABLE 1 Sucker counts, heteromorphic arm tip counts and arm lengths for normal arms and hectocotylized arms (R3) of males of *Eledone caparti*.

Specimen	ARM	Suckers	Modif.	Total	Arm Length (mm)
A.	R1	98	35	133	193
	R2	97	34	131	143
	R3	41	—	41	76
	L3	59	82	141	111
	R4	60	73	133	106
B.	R1	89	36	125	174
	R2	72	63	135	115
	L3	59	77	136	94
	R3	43	—	43	65
	R4	57	80	137	95
C.	R1	85	45	130	179
	R2	54	47	101	104
	R3	41	—	41	64
	L3	REGENERATING			
	R4	41	68	109	78

ber, rather than by the sum of suckers and modifications. Because the modified suckers at the arm tips are very strongly reduced in size, e.g. over 14 can occupy 1 mm in males of *E. caparti*, including them would have biased the results against the hypothesis being tested.

The number of suckers on, and the lengths of, the normal arms of each individual specimen were meaned. To compare the number of suckers on normal arms of octopuses with one sucker row to those with two sucker rows independent of differences in size, the mean number of suckers was plotted versus mean arm length for each individual.

Using arm length as the univariate proxy of size carries with it liabilities. Voight (in press a) hypothesized that the different parts of the muscular octopus body respond to preservation equally, allowing measurements within a preserved specimen to be compared without net preservation bias, as shown by Voight (1991). Because preservation-linked changes affect arm length but not the number of suckers, such biases affect only the x-axis in this analysis. The arms of flaccid specimens may appear abnormally long with comparatively few suckers; contracted arms may appear short with many suckers. To moderate the effect of this bias, a large size range of specimens was included. Arm length rather than a multivariate size measure was used here because it is easily determined, requires no statistical expertise, and is a biologically realistic measure by which to compare the number of suckers.

Data from hectocotyli were analyzed directly. The number of suckers versus hectocotylus length was plotted for male specimens of each species.

RESULTS

On the normal arms of the octopuses considered, virtually all specimens with suckers in double or zigzag rows have more suckers at a given arm length than do those with one row. With few exceptions, points representing specimens with one sucker row can be separated from those representing specimens with two sucker rows by a curve on the plot of sucker number versus arm length (Fig. 1). Specimens of *Eledone cirrhosa* and the type of *Pareledone turqueti*, both with suckers arranged in a zigzag pattern, have more suckers at the same arm length than do congeneric specimens of comparable size with suckers arranged in a single row; they fall on the two-rowed side of the curve.

Four specimens of *Pareledone* and the holotype of *Aphrodoctopus schultzei* violate this pattern. Suckers on these five specimens were arranged in double rows or in zigzags, despite plotting with specimens with a single sucker row (Fig. 1).

Most specimens of *Pareledone* have fewer than 50 suckers on an arm, however, specimens of *P. senoi* (Taki, 1961; Kubodera & Okutani, 1986) diagnosed as the genus *Megaleledone* based on their large size, appear to have up to 65 suckers (Fig. 1). Arms
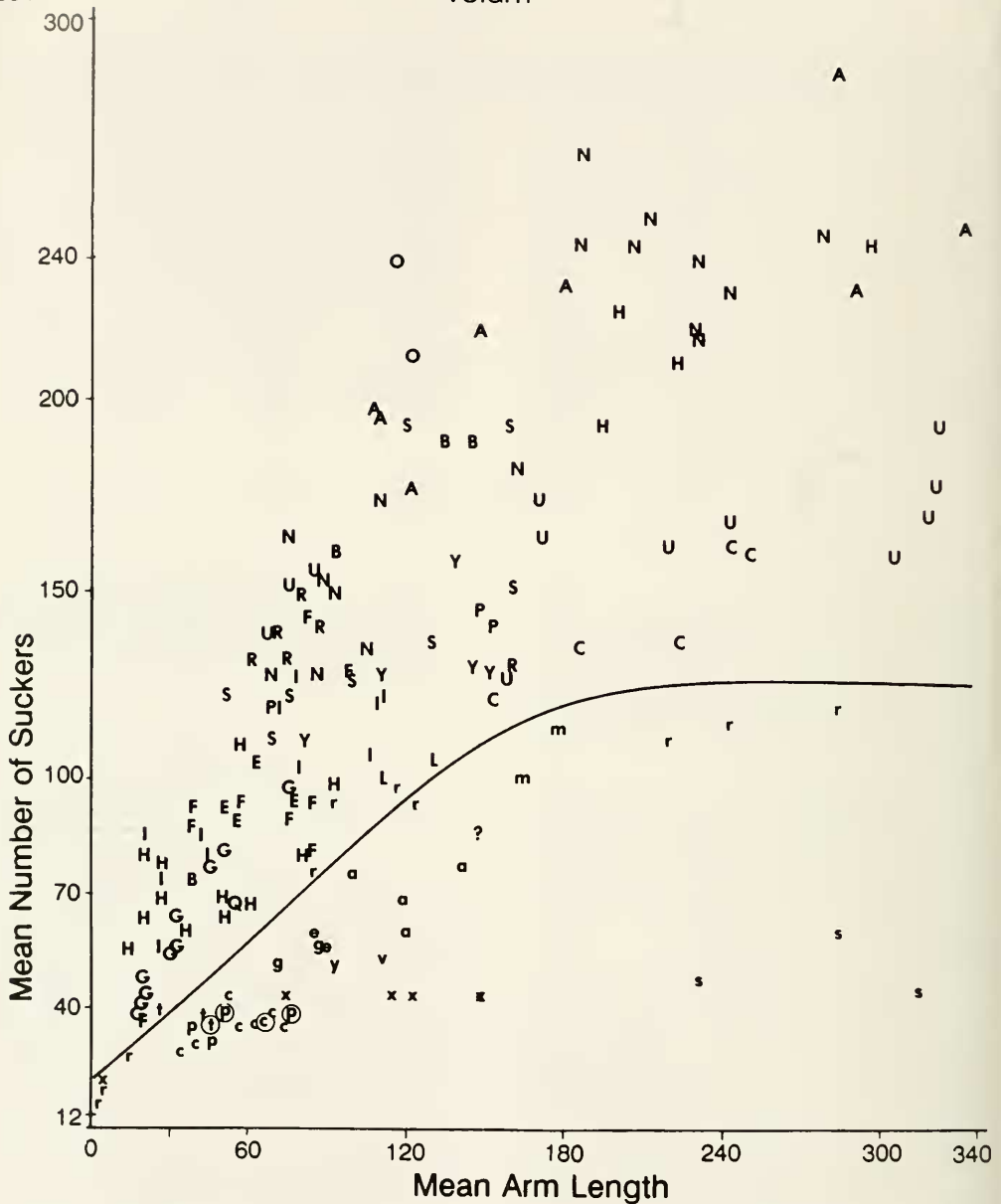
FIG. 1. Plotted for the normal arms of each specimen are the mean number of suckers versus the mean arm length. Upper case letters represent specimens with a double sucker row: A, *Octopus bimaculatus*; B, *O. briareus*; C, *Cistopus indicus*; E, *O. selene*; F, *O. fitchi*; G, *O. chierchiae, O. penicilifer* and *O. stitiochrus*; H, *O. hubbsorum* and *Hapalochlaena* spp., I, *O. digueti*, L, *O. californicus*; N, *Macrotritopus defilippi/horridus*; O, *O. macropus/ornatus*; P, *Pteroctopus tetracirrhus*; Q, *Octopus (Macrochlaena) winckworthi*; R, *Robsonella fontanianus*; S, *Scaeurgus unicirrhus/patagiatus*; U, *O. bimaculoides*; V, *O. vulgaris*; X, *O. filosus*; Y, *O. burryi; ? Aphrodoctopus schultzei*. Lower case letters represent specimens of taxa with a single sucker row: a, *Eledone caparti*; c, *Pareledone charcoti*; e, *Tetracheledone spinicirrus*; g, *E. gaucha*; m, *E. moschata*; p, *P. polymorpha*; r, *E. cirrhosa*; s, *P. (Megaleledone) senoi*; t, *P. turqueti*; v, *Vosseledone charrua*; x, *P. adelieana, P. aurorae P. harrissoni* and *P. nigra* (one specimen each); y, *E. massyae*. The curve, which was fitted by eye, generally separates specimens with a single sucker row (below) from those with two sucker rows and suckers in a zigzag arrangement (above). The points within circles represent specimens of *Pareledone* with suckers in zigzags below the curve.

of specimens of *Eledone* can carry at least 135 suckers; specimens of *Octopus* can have up to 300 suckers on an arm. The number of suckers on an arm of *E. cirrhosa* and *E. moschata* approaches that of some specimens with two sucker rows. The number of suckers on the arms of the type of *P. turqueti* (Joubin, 1905) cannot be distinguished from that of octopuses of equal size with two sucker rows.

Although most octopuses with one sucker row are separated from those with two sucker rows by a very narrow margin (Fig. 1), within each group the average number of suckers borne on an arm of a given length varies considerably. At arm lengths near 200 mm, specimens with one sucker row average from 46 (*P. senoi*) to 112 (*E. moschata*) suckers on an arm, specimens with two sucker rows average from 135 (in *Cistopus indicus*) to 247 (in *Macrotritopus* spp.) suckers on an arm. Literature-based and specimen-based data report a comparable number of suckers on arms of similar length within a taxon.

On the plot of the number of suckers on the hectocotylus versus hectocotylus length (Fig. 2), most males of taxa typified by a single sucker row have fewer suckers on the hectocotylus than do specimens with two sucker rows. On the hectocotyli of two males of *E. cirrhosa*, one with one sucker row and one with zigzag sucker arrangement, however, the number of suckers equals or exceeds that on hectocotyli of octopuses with two rows. The male type of *A. schultzei* with two sucker rows, has as few suckers on the hectocotylus as do males with one sucker row. Hectocotyli with one sucker row, other than those of *Eledone*, always plot beneath the curve that separates normal arms with one from those with two sucker rows; hectocotyli with two sucker rows plot on both sides of the curve.

DISCUSSION

The hypothesis that sucker crowding is associated with the formation of double sucker rows is supported. In most of the octopus specimens considered, if the number of suckers exceeds a critical limit dependent on arm length, the suckers form double rows. The consistency of this limit, or threshold (Fig. 1), among the octopuses considered suggests that a physical constraint affects each of the taxa considered; the five exceptional specimens reveal the effect of other factors.

In four specimens of *Pareledone*, the suck-

ers arranged in zigzags despite being few in number. These specimens may violate the pattern because their arms were preserved straight, in a swimming position, as recommended by Roper & Sweeney (1983). The arms of comparable specimens that are recurved in preservation carry a single sucker row.

In fixation, unrestrained arms recoil, apparently due to contraction of the web. On a recurved arm, the oral, suckered surface on the outer curve of the arm is in tension; the aboral surface, forming the inner curve, is compressed. Artificially straightened arms are subject to different forces, which may invalidate comparisons between straight and recoiled arms. When straight arms are flexed aborally, the space between the suckers increases and their arrangement can approach a single row.

That a curve rather than a line separates most taxa with one sucker row from those with two rows (Fig. 1) illustrates that sucker size also influences the relationship between suckers. On the short arms of young octopuses with small suckers, each small sucker at the arm tip occupies a large proportion of the total space. On longer arms with larger suckers, small suckers at the arm tip occupy proportionately less space, the large suckers already in place dominate. The threshold curves with increasing size as a result of growth.

Sucker growth may also explain why some hectocotylized arms violate the pattern seen in normal arms (Fig. 2). Hectocotyli develop as normal arms up to a point; if more than the critical number of suckers recruit, double sucker rows form. Small hectocotyli plot as predicted by normal arms (Fig. 2), and they are directly comparable; the comparison, however, becomes invalid with growth. The hectocotylus carries an apparently species-specific number of suckers, often many fewer than on normal arms (Toll, 1988; Villanueva et al., 1991). Although hectocotyli are shorter with fewer suckers than are other arms, the arm and suckers continue to grow, as evidenced by within species variation in hectocotylus length (Fig. 2; Toll, 1988; Villanueva et al., 1991). If the suckers on the hectocotylus become larger than those on normal arms, their size may maintain the double sucker rows, despite their reduced number.

If a double sucker row is associated with sucker crowding, and large suckers occupy more space than small suckers, then a comparatively few very large suckers could form
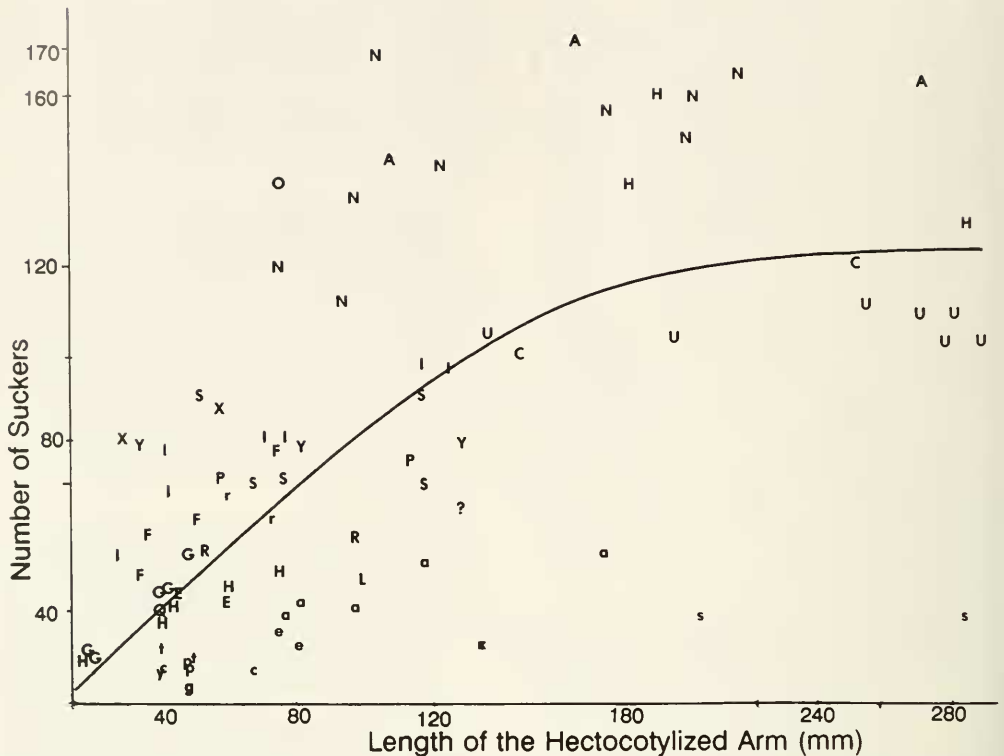
FIG. 2. Plotted are the number of suckers on the hectocotylus versus hectocotylus length. Symbols defined as in Figure 1. The curve separates normal arms with two rows from normal arms with one sucker row.

double rows. This mechanism has been suggested to create double sucker rows in male specimens of the cirrate octopods *Opisthoteuthis depressa* and *O. japonica* (Sasaki, 1929; Taki, 1963). I suggest that this mechanism also produced the double sucker rows on the type of *A. schultzei*. The number of suckers on the arms of the type predicts that it will have a single sucker row, but the 6–8 dramatically enlarged suckers on each arm of *Aphrodoctopus schultzei* (Roper & Mangold, 1991) may occupy enough space that most suckers occupy more than one row (Hoyle, 1910: plate Va, fig. 1; Roper & Mangold, 1991: fig. 4).

Sucker number varies more within groups sharing the same number of sucker rows than it does between groups. Such groups may thus be arbitrary units. Three lines of evidence support this statement. First, although the genera *Eledone* and *Pareledone* are defined by having a single sucker row, specimens of both can have suckers arranged in

two rows or in zigzags (Joubin, 1905; Gravely, 1908). *Octopus*, defined by having a double sucker row, contains specimens with suckers arranged in zigzags or nearly single rows (Robson, 1932). That exceptions occur in diverse genera suggest that the character is artificial.

Second, the muscles attaching the suckers to the arms are very similar in specimens of *Eledone* and *Octopus* (Guérin, 1908; Kier & Smith, 1990). Guérin (1908: 59) predicted that eliminating some of the suckers and elongating the axis of the arm, that is reducing sucker crowding, would shift the sucker arrangement from two rows to one. The present results support his prediction and indicate that these genera differ only superficially in this character. Detailed studies of other genera and of developmental series have yet to be accomplished.

Third, the distribution of points relative to the critical limit separating specimens with a single row from those with double suckers

rows (Fig. 1) reflects the arrangement of suckers on most specimens. Points lying just above the curve (Fig. 1) represent specimens of *Cistopus indicus* that have suckers arranged diagonally, or nearly in a single line (Robson, 1929), as predicted by the plot. Specimens of *Eledone* are just below the curve if the suckers form a single rows; specimens of this species with suckers in a zigzag are just above it. The continuous distribution of points reflects the continuous nature of the character.

If, as suggested here, the spatial relationship among the suckers determines their arrangement, different strategies may serve to influence that relationship. Chief among these strategies may be differentiation of sucker sizes along the arms.

If octopuses have dramatically more than the critical number of suckers required to form double sucker rows, why do the suckers only form double rows? Although individuals with three sucker rows per arm are currently considered developmental anomalies (Toll & Binger, 1991), Owen (1881) named the genus *Tritaxeopus* for specimens with three sucker rows. Owen, who suggested that sucker arrangement was continuous among the Octopodidae, stated that because *Tritaxeopus* differed as much from *Octopus* in sucker row number as did *Eledone*, it merited equal taxonomic recognition. Owen's (1881) report that 286 suckers occupy the 584 mm-long third arm of his now missing type specimen is comparable to specimens included here with shorter arms (Fig. 1) and two sucker rows.

The rarity of specimens with multiple sucker rows may be associated with sucker size differentiation. In specimens with a single sucker row, the suckers occupy a comparatively narrow size range. Especially in specimens of *Pareledone*, the terminal suckers are large compared to those on the tips of arms with two sucker rows. In shallow-water octopuses with two sucker rows, the suckers near the margin of the web are distinctly the largest; distally, sucker size declines dramatically but continuously. Because few suckers are large, the amount of crowding is reduced, as is the crowding associated with the many small suckers. By partitioning sucker size, two discrete sucker rows may be maintained despite the presence of hundreds of suckers. Why multiple sucker rows appear to be avoided by octopuses may relate to functional difficulties or that increased nervous and muscular control are required.

That increased sucker density is associated with double sucker rows is consistent with data available for specimens of the deepwater genus *Benthoctopus* (Voight, unpubl.). Available specimens and data (Russell, 1922) for *Bathypolypus arcticus* and *B. faeroensis* show that despite their suckers being few in number and small in size (Voight, in press) they also form double rows. If the mechanism forming double rows can be shown to differ between *Bathypolypus* and the octopuses considered here, double sucker rows would be shown to be convergent in the Octopodidae, as predicted by Robson's (1932) classification of the family and my preliminary cladogram (Voight, 1990).

If the number of sucker rows is unreliable for phylogenetic reconstruction, could the underlying character suite of sucker number and arm length indicate close evolutionary relationships, e.g. between *Octopus* and *Eledone*? Higher order names have been assigned, not to reflect relationships, but to group outwardly similar taxa by readily apparent characters (e.g. Joubin, 1918). Anatomists who perhaps believed that the generic names indicated distinctly different taxa have compared these genera but have rarely found significant differences (Girod, 1882; Guérin, 1908; Kier & Smith, 1990).

Without an independent means of postulating relationships, and aware that a similarity in the relationship between sucker number and arm length can be produced by changes in either character, conclusions are premature. The number of suckers in *Octopus bimaculatus* and *O. bimaculoides*, very similar species thought to have diverged only recently (Pickford & McConnaughey, 1949), differ more than among species of *Octopus* and *Eledone* (Fig. 1), suggesting that this character does not necessarily reflect evolutionary history.

Eliminating the number of suckers rows as a taxonomic character does not affect most currently recognized genera. The genus *Pareledone* should be defined to reference its few suckers on each arm rather than one sucker row; its definition, however, may still be based solely on plesiomorphic, or ancestral, characters (Voight, 1993). *Eledone* remains as a distinct taxon; its members share the apparent synapomorphies of male heteromorphic arm tips formed by the lateral extension of sucker buds, the reduction or absence of a calamus, the anterior fusion of the branchial retractors and, pending more data, *in utero* fertilization (Perez et al., 1990).

Whether *E. palari* Lu & Stranks, 1991, shares homologous characters is uncertain.

Eledone, however, may not be monophyletic; it appears to share with *Aphrodoctopus* several characters that suggest common ancestry. A single male specimen was designated as type of the genus *Aphrodoctopus* by virtue of its apparent double sucker rows and characters unique in *Octopus* but shared with species in the genus *Eledone*. The type specimen, despite the appearance of having two sucker rows, plots with specimens having one row (Fig. 1), possibly due to its very large suckers, as discussed above.

Characters supporting the relationship between *A. schultzei* and species in *Eledone* include the heteromorphic arm tips of males and the structure of the ligula. Although Roper & Mangold (1991) stress the unusual ligula, the ligulae of males of *E. caparti* appear to be very similar (Adam, 1952: fig. 52), as, to a lesser degree, do those described for *E. thysanophora* by Voss (1962), *E. massyae* by Voss (1964), and for *Pareledone carlgreni* by Thore (1945).

Because the characters cited here as synapomorphies with *Eledone* were the basis for the new genus, and the number of sucker rows is an artifact of sucker size and density, I suggest that *A. schultzei* be placed in *Eledone*. Features distinguishing it from *E. thysanophora* are yet to be determined. The species are likely to be closely related to *E. caparti*; they share the structure of the ligula, sucker size differences, and arm formulae and may have adjacent geographic distributions. The species can be distinguished by the spermatophores; crochets are present in *E. schultzei* and *E. thysanophora* but absent in *E. caparti*.

ACKNOWLEDGEMENTS

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